2013. The Journal of Arachnology 41:374–380

Love is in the air and on the ground: olfactory and tactile cues elicit visual courtship behavior by *Cyrba* males (Araneae: Salticidae)

Ana M. Cerveira[1,3] and **Robert R. Jackson**[1,2]: [1]School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand; [2]International Centre of Insect Physiology and Ecology (ICIPE), Thomas Odhiambo Campus, Mbita Point 40350, Kenya

Abstract. Jumping spiders (Salticidae) are known for their complex eyes and exceptional spatial vision, but less is known about the role of chemoreception in salticid behavior. Here we investigate whether olfactory pheromones (i.e., airborne chemical signals) from conspecific spiders and their draglines elicit the display behavior typically performed during vision-based courtship from the males of *Cyrba algerina* (Lucas 1846) and *C. ocellata* (Kroneberg 1875). We used conspecific and heterospecific spiders and their draglines as potential sources of chemical cues. We show that olfactory cues from conspecific females, but not conspecific males or heterospecific females, effectively elicit vision-based courtship from the males of both *Cyrba* species. These results demonstrate that *C. algerina* and *C. ocellata* males make display decisions on the basis of species- and sex-specific olfactory information. Moreover, even in the absence of a conspecific female spider, female draglines suffice as a source of olfactory pheromones, illustrating the difficulty of ruling out olfaction when testing for chemotactile pheromones.

Keywords: Jumping spiders, mate-identification, olfaction, pheromones

It is common for animals to use pheromones in species and sex identification (Bradbury & Vehrenchamp 2011; Steiger et al. 2011). However, the literature on pheromones is dominated by research on insects (Shorey 1976; Cardé & Millar 2004; Symonds & Elgar 2008), (ref), with considerably less being known about the role of sex pheromones in the biology of spiders (Gaskett 2007; Schulz 2013).

Arachnologists often make a distinction between chemotactile and olfactory pheromones in the spider literature (Barth 2001; Foelix 2011), the former depending on contact chemoreception, and the latter on the detection of airborne volatile compounds. Although experiments that allow for contact chemoreception in the presence of web, nest or dragline silk are common, only a few spider species have been shown experimentally to rely on olfactory communication (Gaskett 2007; Uhl 2013).

Jumping spiders (Salticidae) are better known for their exceptional capacity for spatial vision (Land & Nilsson 2002; Harland et al. 2012), and for their intricate and elaborate vision-based behavior (Foelix 2011), including vision-based courtship displays (Jackson & Pollard 1997). However, numerous examples are also known of salticids expressing refined abilities for using chemical, acoustic, tactile, and percussion signals during intraspecific interactions (Jackson & Pollard 1997; Elias et al. 2010). Although experiments allowing for response to chemotaetile pheromones are more common in the salticid literature (Uhl 2013), 30 species from 17 salticid genera are currently known to use specifically olfactory sex pheromones (Willey & Jackson 1993; Jackson & Cross 2011; Nelson et al. 2012; Cerveira & Jackson 2013).

Our interest here is in a particular cross-modality effect that until now has only been described in one salticid species, *Evarcha culicivora* Wesolowska & Jackson 2003 (Cross & Jackson 2013). In *E. culicivora,* chemoreception elicits vision-based courtship. This cross-modality effect is of particular interest because it appears to be contrary to Foelix's (2011) hypothesis that chemotactile pheromones function primarily by eliciting the spider's courtship displays and olfactory pheromones function primarily by attracting the spider to a potential mate's location.

As a step toward determining how common it is within the Salticidae for pheromones to elicit vision-based display, we carried out experiments using *Cyrba algerina* (Lucas 1846) and *C. ocellata* (Kroneberg 1875). The rationale for using these two species comes from previous research showing that the males of these species are attracted to the odor of conspecific females (Cerveira & Jackson 2013). However, whether chemical stimuli might elicit vision-based displays in these species has not been investigated before.

We have also been interested in the distinction between olfactory and chemotactile pheromones. Two classes of sensory organs mediate chemoreception in spiders. Tip-pore sensilla are specialized hairs on the spider's palps and forelegs that function primarily as contact chemoreceptors (Foelix 1970; Harris and Mill 1973; Tichy et al. 2001; Jiao et al. 2011), whereas tarsal organs are small pits, or sometimes rods, on the dorsal side of each leg tarsus that function primarily as olfactory receptors (Foelix & Chu-Wang 1973; Dumpert 1978; but see Ehn & Tichy 1996). However, when only the spider's behavior is recorded during spider-pheromone experiments, we need to acknowledge the difficulties that can arise when trying to determine whether the behavior observed is mediated by olfaction or by contact chemoreception. Although we can easily rule out contact chemoreception by ensuring that the test spider does not touch the putative source of the chemical stimuli, finding methods that test for chemotactile pheromones while preventing olfaction is a formidable problem. Solving this problem is not our goal, but we illustrate its relevance by showing that dragline odor can elicit vision-based courtship display.

[3]Current address: Centre for Environmental and Marine Studies (CESAM), Faculdade de Ciências, Universidade de Lisboa, Edif. C2, Campo Grande, 1749-016 Lisboa, Portugal. E-mail: ana.cerveira@gmail.com

METHODS

All test spiders were taken from laboratory cultures (second and third generation; origin for *C. algerina*, Sintra, Portugal; for *C. ocellata*, Mbita Point, Kenya). Voucher specimens of *C. algerina* and *C. ocellata* have been deposited at the National Museum of Kenya (Nairobi), the Museum of Natural History (Wroelaw University, Poland) and the Florida State Collection of Arthropods (Gainesville, Florida). We adopted standard spider-laboratory rearing and testing procedures and provide only critical details here. Further details can be found elsewhere (see: Jackson & Hallas 1986; Cerveira & Jackson 2011, 2013).

Spiders were kept individually in clear plastic cages (diameter 55 mm, height 100 mm). A hole in the top was used for introducing prey and another hole covered with a metal screen allowed air to enter the cage. The screen was heat-sealed to the plastic beside the hole. To ensure that the spider always had access to water, we made a hole centered in the bottom of the cage and placed the cage on a plastic pot filled with water. A cotton roll ("dental wick") was positioned in this hole with one end protruding a few millimeters into the cage and the other extending outside the cage into the pot of water. We replaced the cotton rolls whenever mold appeared on them. We also removed prey remains and cleaned the cages frequently. Spiders were maintained on a mixed diet of spiders (*Argyrodes* spp. and *Pardosa* spp.) and non-biting midges (Chaoboridae and Chironomidae) collected from the field as needed.

For environmental enrichment, which is known to be important when rearing salticids for behavioral experiments in the laboratory (Carducci & Jakob 2000), each cage contained a piece of dark cardboard folded in a bellows shape and kept in place inside the cage by a thin bamboo stick that pierced the folds in the cardboard like a skewer (Fig. 1). Resident spiders frequently walked on, and captured prey on, the cardboard. Resident spiders also used the darker recesses in the folded eardboard as nest-building and resting sites. Only adult males were used as test spiders because, consistent with a trend among animals as a whole (Trivers 1972; Andersson 1994), *Cyrba* males are more active than females at displaying during courtship (Jackson 1990).

Our test apparatus was a plastic Petri dish (diameter 60 mm) sitting in the center of a glass-top table (300 mm × 300 mm, glass 5 mm thick). Wooden legs held the table top 270 mm above the laboratory bench (Fig. 2). The Petri dish had two holes (diameter 16 mm), one in its base (stimulus opening) and the other in the lid (entrance opening). The holes were plugged with perforated rubber stoppers. The narrower end of the stopper was the same diameter (16 mm) as the hole and therefore fit evenly with the inner surfaee of the dish. The hole in each stopper held a glass tube (diameter 8 mm; length 45 mm). The tube in the entrance-opening stopper was called the "entrance tube" and the hole in the stimulus-opening stopper was called the "stimulus tube." A matching hole of similar diameter (18 mm) in the tabletop allowed the stimulus tube to fit through the table top and connect via silicone tubing to a glass tube (diameter 15 mm; length 90 mm) called the "odor chamber." The odor chamber was in turn connected via silicone tubing to an air pump. A Matheson FM-1000 flow meter between the pump and the odor chamber maintained

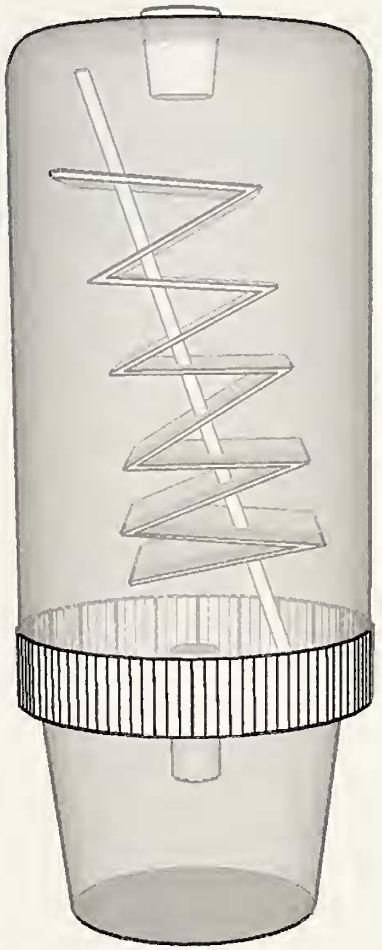

Figure 1.—Salticid maintenance cage. Each cage (diameter 55 mm, height100 mm) contained a piece of dark cardboard folded in a bellows shape kept in place by a thin bamboo stick pierced through the cardboard folds. A hole in the top was used for introducing prey. Water provided via cotton wick partially immersed in water and extending through base of cage.

constant airflow set at 1500 ml/min. There was no evidence to suggest that this airflow setting had any adverse effects on the test spider's behavior. We used nylon netting to cover the openings of the glass tubes and to ensure the spiders could not leave the Petri dish.

Three testing methods were used with both *Cyrba* species: olfactory, tactile and olfactory-tactile tests. In olfactory tests, there was either a source spider or its draglines in the odor chamber, but no draglines were present in the Petri dish. The odor chamber was empty during tactile tests, but the Petri dish contained draglines from the source spider. In olfactory-tactile tests, the odor chamber contained a conspecific female and the Petri dish contained draglines from a heterospecific female. In olfactory tests and in tactile tests, we used males and females of both species as odor sources. However, in olfactory-tactile tests, only female spiders and their draglines provided odor cues.

We collected draglines with a glass Petri dish (diameter 60 mm) lined with two circular sheets of blotting paper (diameter 60 mm), one for the inside base and one for the inside lid. The blotting paper was held in place by four squares (each side 10 mm) of double-sided sticky tape spaced evenly

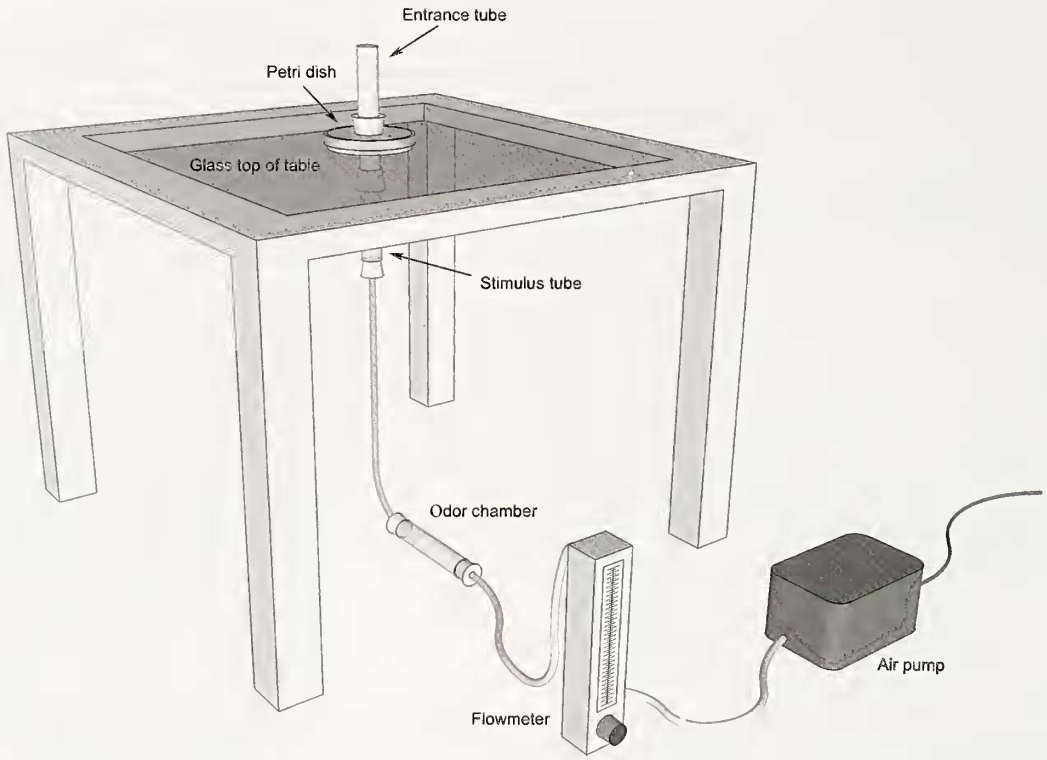

Figure 2.—Apparatus for display-elicitation testing. Three test types were performed: olfactory, tactile and olfactory-tactile. Depending on test type, odor chamber and Petri dish may contain source spider or the source-spider's draglines. See text for details.

around the inside perimeter of the dish. At 0800 h the source spider was put in the dish, and the dish was then oriented upright using a clamp so that neither of the two circles of blotting paper was above the other. Before testing began on the following day, we opened the Petri dish, removed the source spider and the sticky tape, chose one of the two pieces of blotting-paper circles at random and placed this circle silk-side-up on the base of the Petri dish or rolled it up loosely and inserted it into the odor chamber. The odor souree, either a source spider or its draglines, was put in the odor chamber 15 min before testing began.

Test spiders were introduced into the apparatus using a glass tube (length 50 mm, diameter 16 mm) with each end plugged by a rubber stopper. After a 5-min acclimation period, we removed one of the stoppers and inserted the tube into the entrance opening of the Petri dish. If the spider was still in the tube after 2 min, we gently nudged the spider using a soft brush so that it entered the Petri dish.

Data collection began when the spider entered the dish and continued for 10 min. During the test, we recorded all instances of test spiders displaying. We defined 'display' as behavior typically seen in vision-based intraspecific interactions, but only rarely seen in any other context. Here we briefly describe four specific displays (quiver-swim-wave, twitch-abdomen, posture, and dance) that were observed during our experiments, but additional details concerning these displays can be found elsewhere (Jackson 1990). We never saw any of these displays during preliminary testing of *Cyrba* individuals in the apparatus with clean blotting paper in the Petri dish and the odor ehamber empty.

Quiver-swim-wave is a modified form of swim-wave, and swim-wave is characteristic of both sexes of *Cyrba* during normal locomotion. When swim-waving, both sexes of *Cyrba* move their forelegs up and to the side and then, without pausing, move them more slowly down and inward. While moving down and inward, the forelegs move across the substratum. At the end of the cycle, the tarsi of the left and right legs are either pointing forward about parallel to each other or converging toward each other. Quiver-swim-waving is similar to swim-waving except for the distinctive quivering motion of the legs during the down-inward phase. Every test spider that engaged in display performed quiver-swim-waving regardless of whether it also performed any of the other three displays.

A spider twitches its abdomen in bouts lasting 1–10 s. During a bout, the spider repeatedly and rapidly flexes its abdomen up from parallel to the substratum and then, after a momentary pause, forcefully moves it back down to parallel to the substratum.

While walking or standing, the spider postures by holding its forelegs elevated and stationary. The two legs are about parallel to the substratum and to each other, and they point straight ahead or converge somewhat in front of the spider.

Dancing is any of three distinctive styles of stepping. Sometimes the dancing spider traces a zigzagging path forward. At other times, it repeatedly makes a semicircle in one direction and then in the other direction. Another style of dancing consists of repeatedly stepping forward and then backwards. Spiders always posture while dancing.

Experiments were carried out under dim light, since it is known from other studies that *Cyrba* may become non-responsive in olfactometer experiments carried out under high levels of ambient light (Cerveira & Jackson 2011). We placed the apparatus inside a brown wooden box (length 500 mm,

Table 1.—Response by adult males of *Cyrba algerina* and *C. ocellata* in three display-elicitation experiments using conspecific and heterospecific males and females as potential pheromone sources (tactile: draglines present, no additional odor cue present in odor chamber; olfactory: draglines absent, odor cue present in odor chamber; olfactory-tactile: draglines and additional odor cue present in odor chamber). See text and Fig. 2 for details on testing methods. $n = 25$ for each row.

Test	Test spider	Cue in stimulus chamber	Cue in petri dish	No that displayed
Olfactory	*C. algerina* male	*C. algerina* female	None	6
		C. ocellata female	None	0
		C. algerina male	None	0
		C. algerina female draglines	None	3
		C. ocellata female draglines	None	0
		C. ocellata male draglines	None	0
	C. ocellata male	*C. ocellata* female	None	8
		C. algerina female	None	0
		C. ocellata male	None	0
		C. ocellata female draglines	None	3
		C. algerina female draglines	None	0
		C. ocellata male draglines	None	0
Tactile	*C. algerina* male	None	*C algerina* female draglines	18
		None	*C. ocellata* female draglines	0
		None	*C. algerina* male draglines	0
	C. ocellata male	None	*C. ocellata* female draglines	22
		None	*C. algerina* female draglines	0
		None	*C. ocellata* male draglines	0
Olfactory-tactile	*C. algerina* male	*C. algerina* female	*C. ocellata* female draglines	16
	C. ocellata male	*C. ocellata* female	*C. algerina* female draglines	19

width 500 mm, height 500 mm). An opening (width 150 mm, height 500 mm) on one of the box's sides allowed access to the testing apparatus. A black cloth curtain fastened to this side of the box was lowered before testing began. A window (width 150 mm, height 200 mm) cut out of the curtain was used for observing the spider, and the window also allowed some light into the box. During testing, the ambient light level at the Petri dish was approximately 10 cd/m^2 (International Light IL 1400 radiometer in integrated mode).

All testing was carried out between 0800 and 1200 h (laboratory photoperiod 12L:12D, lights on 0700 h). We never used an individual spider more than once in any experiment as a test spider or as a source spider. For standardization, all test and source spiders were unmated adults that had matured 2–3 weeks before testing. The distribution of post-maturation times for each treatment was roughly the same. No spiders had any direct contact with other individuals of either *Cyrba* species before or during testing. For standardizing hunger level, all test and source spiders were kept without food for 4–5 days before testing. We used chi-square tests of independence for comparing data from different experiments (null hypothesis: findings in one experiment same as in another experiment).

RESULTS

Olfactory tests.—As no male spiders from either *Cyrba* species displayed when the odor source was from a conspecific male or a heterospecific female, data from these tests were pooled. When the odor source was a conspecific female, we observed displaying in 24% of the trials in which the test spiders were *C. algerina* and in 32% of the trials when the test spiders were *C. ocellata*. Quiver-swim-waving alone was seen in 50% and 37.5% of the instances of displaying by *C. algerina* and *C. ocellata* males, respectively. In the remaining instances, we saw quiver-swim-waving in conjunction with other display behavior (*C. algerina* – 33.3% postured without dancing, 16.7% twitched their abdomens; *C. ocellata* – 25% twitched their abdomens, 25% twitched their abdomens and also postured, 12.5% postured without dancing and also while they danced).

When the odor sources were the draglines of conspecific females, 12% of the test spiders of both species displayed. Of the test spiders that displayed, 33% of these individuals quiver-swim-waved only, 33% also postured and 33% also twitched their abdomens.

Significantly more males displayed when the odor came from a conspecific female or a conspecific female's draglines instead of from a heterospecific female or a conspecific male (*C. algerina* – odor of a conspecific female, $X^2 = 13.04$, $P < 0.001$; odor of a conspecific female's draglines, $X^2 = 6.25$, $P < 0.05$; *C. ocellata* – odor of a conspecific female, $X^2 = 17.91$, $P < 0.001$; odor of a conspecific female's draglines, $X^2 = 6.25$, $P < 0.05$; Table 1). Although odor from conspecific females elicited display more often than odor from conspecific females' draglines, the difference was not significant for either *C. algerina* ($X^2 = 1.22$, $P = 0.269$) or *C. ocellata* ($X^2 = 2.91$, $P = 0.081$).

Tactile tests.—As no male spiders displayed when the draglines were from conspecific males or heterospecific females, we pooled data from these tests. However, when the draglines used came from conspecific females, most *Cyrba* males displayed (*C. algerina*: 72% of tests; *C. ocellata*: 88% of tests). Significantly more test spiders displayed in tactile tests when the draglines were from conspecific females instead of heterospecific females or conspecific males (*C. algerina*, $X^2 = 47.37$, $P < 0.001$; *C. ocellata*, $X^2 = 62.26$, $P < 0.001$).

Quiver-swim-waving alone was seen in 66.7% and 50% of the instances of displaying by *C. algerina* and *C. ocellata*, respectively. In the remaining instances, we observed quiver-swim-waving in conjunction with other display behavior

(*C. algerina* – 11.1% postured without dancing, 11.1% twitched their abdomens, 11.1% twitched their abdomens and also postured without dancing; *C. ocellata* – 27.3% postured without dancing, 13.6% twitched their abdomens, 4.6% postured without dancing and also while they danced, 4.6% twitched their abdomens and also postured without dancing and while they danced).

Olfactory-tactile tests.—When the odor chamber housed a conspecific female and there were draglines of a heterospecific female in the Petri dish, *C. algerina* and *C. ocellata* males displayed in 64% and 76% of the tests, respectively. Quiver-swim-waving alone was seen in 56.3% and 63.2% of the instances of displaying by *C. algerina* and *C. ocellata* males, respectively. In the remaining instances, quiver-swim-waving was seen in conjunction with other display behavior (*C. algerina* – 12.5% postured without dancing, 12.5% twitched their abdomens, 12.5% twitched their abdomens and also postured without dancing, 6.2% twitched their abdomens, postured without dancing and also while they danced; *C. ocellata* – 10.5% postured without dancing, 15.8% twitched their abdomens, 5.3% postured without dancing and also while they danced, 5.3% twitched their abdomens, postured without dancing and while they danced).

Comparisons.—When cues came from conspecific females, significantly more *Cyrba* males displayed during tactile tests than during olfactory tests (for olfactory tests, we pooled data from tests in which the odor source was a spider in the odor chamber with data from tests in which the odor source in the odor chamber was only the spider's draglines; *C. algerina*, $X^2 = 21.09$, $P < 0.001$; *C. ocellata*, $X^2 = 29.46$, $P < 0.001$).

The number of *Cyrba* males that displayed in olfactory-tactile tests (i.e., tests in which males could touch a heterospecific female's draglines while in the presence of the odor from a conspecific female) was significantly higher than the number of males that displayed during olfactory tests (i.e., tests in which a conspecific female spider was the odor source in the odor chamber and there were no draglines from another spider in the Petri dish) (*C. algerina*, $X^2 = 8.12$, $P < 0.05$; *C. ocellata*, $X^2 = 9.74$, $P < 0.05$).

Significantly more *Cyrba* males displayed in olfactory-tactile tests than in tactile tests in which the draglines they could touch came from heterospecific females (*C. algerina*, $X^2 = 23.53$, $P < 0.001$; *C. ocellata*, $X^2 = 30.65$, $P < 0.001$). However, the number of males that displayed during tactile tests in which the draglines came from conspecific females was not significantly different from the number that displayed during olfactory-tactile tests (*C. algerina*, $X^2 = 0.37$, $P = 0.544$; *C. ocellata*, $X^2 = 1.22$, $P = 0.269$).

DISCUSSION

Male *C. algerina* and *C. ocellata* initiated courtship when placed in a Petri dish in which a conspecific female had been present, but not when a heterospecific female or a conspecific male had been present. This type of evidence is commonly used for concluding that conspecific female draglines carry chemotactile pheromones and that these pheromones elicit male courtship behavior. If the tactile trials had been the only trials we carried out, we might have overlooked how tactile trials did not actually rule out olfaction. However, the fact that *Cyrba* males also displayed when they could not touch the draglines, but could detect the odor of draglines, suggests that female draglines also carry olfactory pheromones, and that these alone can elicit vision-based display behavior.

Knowing that the draglines of conspecific females are a source of olfactory pheromones, regardless of whether they are also a source of chemotactile pheromones, makes the outcome of taetile testing on its own more difficult to interpret. Our findings show that significantly more males initiated courtship during tactile tests than during olfactory tests. One possible explanation for this result is that tactile tests provided *Cyrba* males with two chemical-cue types (chemotactile and olfactory) instead of a single one (olfactory) and that the additive effects from these two kinds of chemical stimulation caused responses to be more frequent when draglines were present in the Petri dish.

However, results from olfactory-tactile tests suggest a different hypothesis. In these trials, the male was exposed to the odor of a conspecific female while in the presence of draglines from a female heterospecific. On their own, heterospecific female draglines did not elicit display during olfactory or tactile testing, suggesting that chemical cues from heterospecific females are not relevant to the male's display decisions. Yet the number of males that initiated vision-based display behavior in olfactory-tactile tests when using heterospecific female draglines was similar to the number of males that displayed during tactile tests using conspecific female draglines, and significantly higher than in olfactory tests when conspecific females were used as the odor source.

Hence, results from olfactory-taetile testing suggest that detecting purely tactile stimuli by touching draglines can increase a male's inclination to initiate courtship even when these are draglines from heterospecific females. It should be noted, however, that the heterospecific females used in our experiments were congeneric with the male test spiders and as such our experiments do not rule out an alternative hypothesis. Males might detect the pheromones present on the draglines of heterospecifc females, but these heterospecific pheromones might not suffice as courtship-eliciting stimuli; rather, they may have an additive effect when combined with the pheromones from a conspecific female in the odor chamber.

More experimental work is needed that aims at determining the actual origin of the pheromones generally attributed to draglines. Typically the salticid is left with blotting paper on which to deposit draglines. As draglines seem to be the dominant deposit left by spiders, it is convenient to attribute the results of these experiments to dragline-associated pheromones, but it is important to rule out the possibility that other deposits (e.g., feces) provide pheromone sources. Another possibility is that the blotting paper becomes impregnated with olfactory pheromones from the female spider's body and that these pheromones might also influence the test spider's behavior during tactile tests.

Although the males of 30 salticid species are known to be attracted to the odor of conspecifie females in olfactometer experiments (Nelson et al. 2012), adoption of vision-based courtship in response to female conspecific chemical signals has only been shown for three of them, *C. algerina* and *C. ocellata* in the present study and *E. culicivora* in an earlier study (Cross & Jackson 2013). However, in addition to vision-based

displays, many salticids, including *C. algerina* and *C. ocellata*, are also known to adopt a non-visual mode of courtship during encounters at nests or webs under dim light. Experiments have shown that, even in the absence of a resident female, contact with nest or web silk from conspecific females elicits male non-visual courtship behavior (Jackson 1987; Jackson & Pollard 1997). However, species from the genus *Cyrba* may be inclined to capture prey (Guseinov et al. 2004; Cerveira & Jackson 2011) and display under dim light to an extent that is unusual for salticids (Cerveira & Jackson unpublished data). An unusual level of activity under dim light might make olfactory pheromones that alert males to the presence of unseen prospective mates unusually important.

We are currently investigating a hypothesis, which, if confirmed, would be an example of males using a mate-locating tactic similar to a predatory tactic ('speculative hunting'; see Curio 1976) adopted by another salticid, *Portia fimbriata* (Doleschall 1859). In the presence of a particular prey odor, *P. fimbriata* is known to make undirected leaps. This behavior stimulates the prey to orient toward the leaping predator, revealing its location (Clark et al. 2000). We propose that, by initiating visible courtship after detecting pheromones in the absence of a visible target, *Cyrba* males solicit a response (i.e., displaying or becoming more active) by a not-yet-seen female, thereby making the female more easily seen by the male.

ACKNOWLEDGMENTS

We thank Godfrey Otieno Sune, Stephen Abok Aluoch and Jane Atieno Obonyo for their assistanee at ICIPE and three reviewers for comments on an early version of the manuscript. We also gratefully acknowledge support of grants from the Royal Society of New Zealand [Marsden Fund (M1096, M1079) and James Cook Fellowship (E5097)] and the National Geographic Society (8676-09, 6705-00).

LITERATURE CITED

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

Barth, F.G. 2001. A Spider's World: Senses and Behavior. Springer, Berlin.

Bradbury, J.W. & S.L. Vehrenchamp. 2011. Principles of Animal Communication. Second edition. Sinauer Associates, Sunderland, Massachusetts.

Cardé, R.T. & J.G. Millar. 2004. Advances in Insect Chemical Ecology. Cambridge University Press, Cambridge, UK.

Carducci, J.P. & E.M. Jakob. 2000. Rearing environment affects behaviour of jumping spiders. Animal Behaviour 59:39–46.

Cerveira, A.M. & R.R. Jackson. 2011. Interpopulation variation in kairomone use by *Cyrba algerina*, an araneophagic jumping spider from Portugal. Journal of Ethology 29:121–129.

Cerveira, A.M. & R.R. Jackson. 2013. Love is in the air: olfaction-based mate-odour identification by jumping spiders from the genus *Cyrba*. Journal of Ethology 31:29–34.

Clark, R.J., D.P. Harland & R.R. Jackson. 2000. Speculative hunting by an araneophagic salticid spider. Behaviour 137:1601–1612.

Cross, F.R. & R.R. Jackson. 2013. The functioning of species-specific olfactory pheromones in the biology of a mosquito-eating jumping spider from East Africa. Journal of Insect Behavior 26:131–148.

Curio, E. 1976. The Ethology of Predation. Springer, New York.

Dumpert, K. 1978. Spider odor receptors: electrophysiological proof. Experientia (Basel) 34:754–756.

Ehn, R.H. & H. Tichy. 1996. Response characteristics of a spider warm cell: temperature sensitivities and structural properties. Journal of Comparative Physiology A 178:537–542.

Elias, D.O., S. Sivalinghem, A.C. Mason, M.C.B. Andrade & M. Kasumovi. 2010. Vibratory communication in the jumping spider *Phidippus clarus*: substrate-borne courtship signals are important for male mating success. Ethology 116:990–998.

Foelix, R.F. 1970. Chemosensitive hairs in spiders. Journal of Morphology 132:313–334.

Foelix, R.F. 2011. Biology of Spiders. Third edition. Oxford University Press, Oxford, UK.

Foelix, R.F. & I.-W. Chu-Wang. 1973. The morphology of spider sensilla. II. Chemoreceptors. Tissue and Cell 5:461–478.

Gaskett, A.C. 2007. Spider sex pheromones: emission, reception, structures, and functions. Biological Reviews 82:27–48.

Guseinov, E.F., A.M. Cerveira & R.R. Jackson. 2004. The predatory strategy, natural diet, and life cycle of *Cyrba algerina*, an araneophagic jumping spider (Salticidae: Spartaeinae) from Azerbaijan. New Zealand Journal of Zoology 31:291–303.

Harland, D.P., D. Li & R.R. Jackson. 2012. How jumping spiders see the world. Pp. 133–164. *In* How Animals See the World: Comparative Behavior, Biology, and Evolution of Vision. (O. Lazareva, T. Shimizu & E.A. Wasserman, eds.). Oxford University Press, New York.

Harris, D.J. & P.J. Mill. 1973. The ultrastructure of chemoreceptor sensilla in *Ciniflo similis* (Araneida, Arachnida). Tissue and Cell 5:679–689.

Jackson, R.R. 1987. Comparative study of releaser pheromones associated with the silk of jumping spiders (Araneae, Salticidae). New Zealand Journal of Zoology 14:1–10.

Jackson, R.R. 1990. Predatory versatility and intraspecific interactions of *Cyrba algerina* and *C. ocellata*, web-invading spartaeine jumping spiders (Araneae, Salticidae). New Zealand Journal of Zoology 17:157–168.

Jackson, R.R. & F.R. Cross. 2011. Olfactory sex and species discrimination by *Portia*, a genus of araneophagic jumping spiders. Journal of Arachnology 39:439–443.

Jackson, R.R. & S.E.A. Hallas. 1986. Predatory versatility and intraspecific interactions of spartaeine jumping spiders (Araneae: Salticidae): *Brettus adonis*, *B. cingulatus*, *Cyrba algerina* and *Phaeacius* sp. indet. New Zealand Journal of Zoology 13:491–520.

Jackson, R.R. & S.D. Pollard. 1997. Jumping spider mating strategies: sex among cannibals in and out of webs. Pp. 340–351. *In* Mating Systems in Insects and Arachnids. (J.C. Choe & B.J. Crespi, eds.). Cambridge University Press, Cambridge, UK.

Jiao, X., Z. Chen, H. Du, J. Chen & F. Lu. 2011. Chemoreceptor distribution and relative importance of male forelegs and palps in intersexual chemical communication of the wolf spider *Pardosa astrigera*. Chemoecology 21:45–49.

Land, M.F. & D.E. Nilsson. 2002. Animal Eyes. Oxford University Press, Oxford, UK.

Nelson, X.J., C.M. Warui & R.R. Jackson. 2012. Widespread reliance on olfactory sex and species identification by Lyssomanine and Spartaeine jumping spiders. Biological Journal of the Linnaean Society 107:664–677.

Schulz, S. 2013. Spider pheromones – a structural perspective. Journal of Chemical Ecology 39:1–14.

Shorey, H.H. 1976. Animal Communication by Pheromones. Academic Press, New York.

Steiger, S., T. Schmitt & H.M. Schaefer. 2011. The origin and dynamic evolution of chemical information transfer. Proceedings of the Royal Society B 278:970–979.

Symonds, M.R.E. & M.A. Elgar. 2008. The evolution of pheromone diversity. Trends in Ecology and Evolution 23:220–228.

Tichy, H., E. Gingl, R. Ehn, M. Papke & S. Schulz. 2001. Female sex pheromone of a wandering spider (*Cupeuius salei*): identification and sensory reception. Journal of Comparative Physiology A 187:75–78.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136–179. *In* Sexual selection and the descent of man. (B. Campbell, ed.). Aldine, Chicago.

Uhl, G. 2013. Spider olfaction: attracting, detecting, luring and avoiding. Pp. 141–157. *In* Spider Ecophysiology. (W. Nentwig, ed.). Springer, Berlin.

Willey, M.B. & R.R. Jackson. 1993. Olfactory cues from conspecifics inhibit the web-invasion behaviour of *Portia*, a web-invading, araneophagic jumping spider (Araneae, Salticidae). Canadian Journal of Zoology 71:1415–1420.

Manuscript received 10 June 2012, revised 25 June 2013.